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# A large-mammal site in a meandering fluvial context (Fonelas P-1, Late Pliocene, Guadix Basin, Spain). Sedimentological keys for its paleoenvironmental reconstruction

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## Abstract

The Fonelas P-1 large-mammal site is located stratigraphically in the youngest unit (Late Pliocene─Pleistocene) of the endorheic fill of the Guadix Basin (Betic Cordillera). At the site location this unit is represented by fluvial sediments of the basin's axial drainage system. The general succession of the site consists of stacked fining-upward cycles, basically beginning with gravel and/or sand filling a meandering channel and concluding with floodplain mud and carbonate. Each of the cycles is made up of four facies associations determined by sedimentological analysis of the sections measured in the paleontological excavation of the site. These associations correspond to sedimentation in definite areas of the fluvial system: (A) filling of a sinuous channel at maximum activity, (B) levee deposits, (C) abandoned channel and (D) floodplain. In the cycle in which the site is located there is a fifth association (E), where the main fossil concentration is found (Fonelas P-1). This is a facies bioturbated by mammals moving over sediments of the abandoned channel association (C). By space-time reconstruction

of the fluvial environments, we can infer that the morphological depression caused by a meander abandonment due to chute cut-off was used as a hyena den. The animal settlement ended when overflow from the laterally migrating active channel began to bury the abandoned meander with floodplain sediments.

*Keywords:* Continental palaeogeography; Fluvial sedimentology; Guadix Basin; Mammals; Pliocene─Pleistocene.

## 1. Introduction

The Fonelas P-1 site (Arribas et al., 2001), located in the Guadix Basin (Betic Cordillera), contains a vertebrate fossil assemblage consisting mainly of large-mammal fossil remains - as well as small minority of amphibians, reptiles, small mammals and birds - which can be used to date it to the Late Pliocene, near the Pleistocene boundary (Late Villafranquian, ca 1.8 Ma).

In three seasons of systematic excavation, almost two thousand bone fragments were recovered. Many are anatomically complete to a high degree (allowing their taxonomic classification), which leads us to consider this as the most important large-mammal site from the end of the Pliocene in the entire Iberian Peninsula.

Analysis of first and last appearance data (FAD and LAD) of the species identified to date corroborates the initial hypothesis of the time-scale being on the Pliocene─Pleistocene boundary (1.9─1.7 Ma) in zones MNQ18─MNQ19.

The faunal assemblage to date identified at this site consists of 32 species of mammals (Mammalia). Three groups of large mammals have been identified according to their paleobiogeographic origin and the time-scale of their incorporation into the Iberian paleomastocenosis: i) a group of animals typical of the latest Late Pliocene in Europe, some of which extended from Asia into these ecosystems around 2.6─2.5 Ma, with species such as *Vulpes alopecoides*, *Acinonyx pardinensis*, *Megantereon cultridens*, *Homotherium latidens*, *Croizetoceros ramosus*, *Cervus? rhenanus philisi*, *Eucladoceros* sp., *Equus major*, *Stephanorhinus etruscus* and *Mammuthus meridionalis*; ii) a second mammal association of Asian origin reaching these latitudes during the Pliocene─Pleistocene transition, such as *Canis etruscus*, *Leptobos etruscus*, *Praeovibos* nov. sp. and *Mitilanotherium* nov. sp.; iii) a third group native to Africa which also

reached the Iberian Peninsula during the Pliocene─Pleistocene boundary, with forms such as *Hyaena brunnea* and *Potamochoerus* nov. sp.. There is also a fourth group of animals at Fonelas P-1 of uncertain origin (either Asian or African) that reached Atlantic Europe in the same brief interval (*Canis* cf. *falconeri* and *Pachycrocuta brevirostris*). Thanks to the quality of the paleontological remains, their extraordinary state of preservation and the abundance of skeletal elements, advanced taxonomic study has led to verification of the presence of new species of the genera *Meles*, *Canis*, *Gazella?*, *Gazellospira*, *Praeovibos*, *Mitilanotherium, Capra* and *Potamochoerus*.

As this is the only known paleontological record with such a variety of species of such diverse origin, the large-mammal assemblage at Fonelas P-1 holds extremely interesting information for the reconstruction of the main migratory routes and the interrelations between African and Eurasian species. In addition, the high scientific interest in this site is due to the fact that, because of the time-scale and combined presence of African and Caucasian species, it is the only site in western Europe similar to the Caucasian site at Dmanisi (Gabunia et al., 2000). Fonelas P-1 is, therefore, the first evidence in Europe to allow definition of the paleoenvironmental framework of the Pliocene─Pleistocene transition, when the first humans spread beyond Africa. As such, therefore, attention should be drawn to the considerable similarities between the sedimentary environment of Fonelas P-1 and the recently reconstructed context of the sites of the earliest stone tool makers in the Awash River Basin, Ethiopia (Quade et al., 2004).

The aim of this paper is to analyze in detail the geological context in which the remains of large mammals accumulated, not just by determining the sedimentary environment, but also by carrying out a reconstruction of the series of geological events before, during and after the concentration of the bone remains. Following Behrensmeyer (1988), we aim to reconstruct the alluvial architecture in which the organic remains accumulated. We thus attempt to draw up a hypothesis that includes the geological factors that resulted in such an exceptional fossil assemblage at a precise place and a very specific time. We hope this model will be of use as a prospecting criterion in this and other basins since, as shown below, the palaeogeographic context of this site has many points in common with those attributed to other vertebrate sites of different ages described in other parts of the world (Badgley and Behrensmeyer, 1995; Willis and Behrensmeyer, 1995, among others).

## 2. Methodology

The fossil-bearing layer (average thickness 20 cm to a maximum of 40 cm) was excavated in 2001, 2002 and 2004. Systematic paleontological excavation followed the classic methodology for analysis of this type of sites, using a grid of $1m^2$ squares (Fig. 1). The field data recorded for each fossil element were: date, stratigraphic log, surface/depth, symbol, size in millimetres (length, width and depth), marks [abrasion/polished, weathering stage (0-1, 2-3, 4-5), roots, dissolution, insects], breakage (longitudinal, spiral, fossil diagenetic), trace [rodents (micro, macro), carnivores (canids, felids, hyaenids)], hominids (chop-marks, cut-marks, etc), trampling marks, colour, colour congruence/sediment, anatomical element (tooth, bone, splinter; bone name; complete, proximal, shaft, distal), side (left, right), taxa (48 possibilities), age (infant, young, adult, senile), joint, association, sedimentary filling, filling congruence, cartography (direction, slope, X, Y, Z), remarks and photograph. This set of field variables was verified in the laboratory and, once the fossils were restored and consolidated, completed by descriptive and metric characterization of taxonomic and taphonomic features.

The taxonomic study (Arribas et al., 2004; Garrido, 2006) was carried out using classic paleontological methods, based on direct observation and morphological comparison with other fossil or present-day records, including metrical analysis to bear out or reject the results obtained by the anatomical study of the taxon to be classified. Biometrical results in no case prevail over anatomical results in taxonomic identification. The procedures used in this study do not therefore differ substantially from those generally used by specialists in large-mammal palaeontology. Biometrical data were acquired in the same way for all groups, using a Sylvac RS 232 digital gauge with 0.01 mm precision. The dental study was carried out using criteria generally used by specialists in the group in question. For most groups the postcranial skeleton was examined following Von der Driesch (1976).

Taphonomic analysis is still in progress, following criteria and emphasizing variables applied in research on other Pliocene─Pleistocene sites (Arribas and Palmqvist, 1998, 2001; Palmqvist and Arribas, 2001; Palmqvist et al., 2002). The methodology has been widened, mainly as regards descriptive variables and their links with sedimentological aspects of our own research project. However, it is still too early to make very precise palaeoecological interpretations, as the samples recovered from Fonelas P-1, although

significant, are not yet sufficient in either number of remains or minimum number of individuals (Arribas and Palmqvist, 1998; Palmqvist et al., 2003). The approximately 30 $m^2$ excavated to date, yielding 2000 fossils, 84% of which are anatomically and taxonomically identifiable elements while the other 16% are indeterminate fragments, are only a small part of the site (800 $m^2$). Future seasons are therefore expected to broaden the spectrum of taxonomic diversity, possibly to include *Hystrix*, *Ursus*, *Macaca*, *Theropithecus*, *Homo* and *Hippopotamus*, among others. We calculate that palaeoecological research can begin after three more seasons of systematic excavation.

The present paper centres on the geological contextualization of the site and the interpretation of the processes affecting the sediments in which the bone remains are found, as well as the deposits immediately preceding and following the organic accumulation. The sedimentological interpretation was carried out using the following procedures:

- Logging a vertical profile containing the entire stratigraphic succession of Unit VI of the basin filling (see section 4) at the position of the site. The data were measured on a 1:50 scale, but are presented in simplified form here.
- Making five detailed 1:10 scale stratigraphic logs.
- Establishing correlations between the detailed stratigraphic logs.
- Identification of simple lithofacies and their associations.
- Architectural elements analysis, following Miall (1985, 1996), to determine the 3-D distribution of the lithofacies and their associations and also identify and classify the sedimentary interruption surfaces.

## 3. Overview of palaeontological data

Out of all the new sites located by our team since 2001 in this area of the Guadix basin (48 locations with large-mammal records, Arribas et al., 2004, and unpublished data from the 2005 season), the Fonelas P-1 site has proved to be especially rich in number and diversity of large mammal remains. It is significant that most of the taxa identified at this location are represented by both cranial elements (mainly complete crania, half maxillas and half lower jaws) and parts of the postcranial skeleton (bones of the spine and limbs) that in many cases can be identified as belonging to the same individual. Isolated teeth are rare in this record. They represent only 10% of the total sample and often appear either fragmented with traces of gastric dissolution (teeth

belonging to grazing animals such as *Equus*, *Gazellospira* or *Leptobos*), or complete, in a site position vertical to the alveolar region of their corresponding crania (belonging to carnivores such as *Canis* and *Hyaena*).

The faunal assemblage identified at Fonelas P-1 to date consists of 2 reptiles, 1 bird, 8 small mammals and 24 large mammals (see Table 1).

The provisional assemblage of this site is heterogeneous as regards the palaeobiogeographic significance of the identified taxa and also their biochronological significance, according to the data known before discovery in 2001 (Azzaroli, 1983, 1995; Azzaroli et al., 1988; Torre et al., 1992, 1996; Arribas and Palmqvist, 1999; Arribas et al., 2001, 2004; Garrido, 2006).

Within this assemblage appear: (a) autochthonous Eurasian taxa, found in other Upper Pliocene–Lower Pleistocene records of the continent: *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Eucladoceros* sp., *Cervus? rhenanus phillisi*, *Homotherium latidens*, *Acinonyx pardinensis*, *Croizetoceros ramosus*, *Lynx pardinus* and *Vulpes alopecoides* ; (b) new species or subspecies of *Gazellospira*, *Megantereon cultridens* and *Meles* native to the Iberian Peninsula; (c) species of Asian genera *Mitilanotherium* and *Praeovibos* new to the Iberian Peninsula; (d) species of African genera *Potamochoerus*, *Capra* and *Canis* new to the Iberian Peninsula; (e) immigrant Asian species found in other European records of the Pliocene–Pleistocene boundary: *Equus major* and *Leptobos etruscus*; (f) immigrant African species found in other European records of the Pliocene–Pleistocene boundary: *Pachycrocuta brevirostris* and *Canis* cf. *falconeri*; (g) an immigrant African species unknown in Eurasia: *Hyaena brunnea* and (h) a taxon of unknown origin: *Gazella?*.

In view of the foregoing, the taxonomic study of Fonelas P-1 will lead to interesting paleontological discoveries regarding faunal turnover and distribution in time of different groups across the European Pliocene–Pleistocene boundary.

Taphonomic interpretation of the site is premature, as there are still insufficient samples and the study is part of a Ph.D. thesis in progress. However, the data obtained during the 2001 and 2002 seasons (NISP 1375) allow us to hypothesize that this is an accumulated association (accumulated taphonomic stage) with a very short period of subaerial exposure before burial, in which scavenging carnivore activity was essential during the biostratinomic stage (secondary association collected by scavengers according to data by Palmqvist and Arribas, 2001).

As can be deduced from the integration of the provisional values of the descriptive taphonomic variables (Table 2), we can discard predators, as well as physical agents, as concentrators of the bone association, excluding therefore the possibility of a primary association collected by the former. Thus, we postulate that the site is the result of the occupation of this particular section of the territory by a hyaenid clan, probably belonging to *Pachycrocuta brevirostris*, as it is the only eudemic hyaenid in the assemblage (deciduous dentition record). The site could have been a feeding area or den where the hyenas collected and modified numerous skeletal remains of the animals they scavenged. The feeding habits of this extinct hyaenid are well known in the fossil record (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001; Mazza and Bertini, 2004) and their presence (Howell and Petter, 1980) and taphonomic identification (Arribas, 1999) are constant across the Pliocene─Pleistocene boundary and during the beginning of the European Pleistocene.

The provisional values of the taphonomic and stratigraphic variables in the Fonelas P-1 samples differ clearly from the characteristics of other sites in this and other continental basins, where the principal cause of site genesis is surface processes (concentration, selection and burial of bone remains by water currents in circum-lake environments, e.g., Huélago, Huéscar-1 and Cúllar de Baza-1; Alberdi et al., 2001). However, the taphonomic features of the Fonelas P-1 sample are similar to the specific attributes of the feeding area or hyena den characteristic of *Pachycrocuta brevirostris* (type site Venta Micena; Arribas and Palmqvist, 1998). The taphonomic research in progress will verify this hypothesis and evaluate the existing paleontological bias and its significance.

## 4. Geological context and stratigraphic location of the site

The Betic Cordillera occupies a large part of the southern Iberian Peninsula and, together with the North-African Rif, represents the western extreme of the belt of Alpine chains around the Mediterranean. It has two main structural domains: the Internal Zones or Alboran Block (Andrieux et al., 1971) located to the South, and the External Zones to the North, representing the deformed South Iberian paleomargin (Vera, 2001). Neogene─Quaternary basins, one of which is the Guadix Basin (Fig. 2), developed on both these domains, beginning in the Late Miocene, and trapped the

sediments resulting from the erosion of the relief in the Internal and External Zones (Viseras et al., 2005).

The Guadix Basin is located in the central sector of the Betic Cordillera (Fig. 2) and occupies some 4600 $km^2$ on the contact between the Internal and External Zones. The basin's sedimentary fill (Fig. 3) has been divided into six genetic units (Fernández et al., 1996a) whose boundary unconformities are related to both tectonic events and eustatic changes (Soria et al., 1998, 1999). The two lower units (Units I and II) are Late Tortonian, corresponding to a stage of marine sedimentation, and the third (Unit III) includes sediments deposited during sea retreat from the central sector of the Betic Cordillera at the end of the Tortonian. The three youngest units (Units IV, V and VI), according to biochronological data, cover the Late Turolian to the Late Pleistocene, which was a period of exclusively continental sedimentation in an endorheic (a basin with internal drainage, where no surface drainage reaching the ocean can be detected) basin context (Fernández et al., 1993; Viseras and Fernández, 1994, 1995; Viseras et al., 1998). This sedimentary stage was interrupted in the Late Pleistocene, when a geomorphological inversion of the basin took place and it was captured in its entirety by the drainage network of the Guadalquivir River, becoming an exorheic domain mainly subjected to erosion (Viseras and Fernández, 1992; Calvache and Viseras, 1997). The Fonelas P-1 large-mammal site is dated by biochronology to 1,800,000 yr B.P. (Arribas et al., 2004) and forms part of the continental sediments of Unit VI (Late Pliocene─Late Pleistocene).

## 5. Palaeogeography and local sedimentary context

Using both the origin of the sediment supply and analysis of sedimentary facies during the continental filling of the basin, two sectors with different depositional characteristics have been differentiated (Vera, 1970): the eastern sector, mostly occupied by a large shallow lake acting as base level for the whole basin, and the western sector, dominated by alluvial fans and fluvial plains, draining towards the eastern lake (Fig. 4). Three main drainage systems have been distinguished in this western sector, where the Fonelas P-1 site is located. They are described below.

Lying approximately parallel to the axis of the basin, the Axial System (Fernández et al., 1993; Viseras and Fernández, 1994) is represented by a broad fluvial valley through which the main drainage to the eastern lake took place. In its proximal zone this system

connects with alluvial fans lying at the foot of the Sierra Nevada relief. The rest of it consists of a floodplain crossed by high sinuosity channels (meandering rivers) and occasionally occupied by shallow ephemeral lakes and palustrine areas (Viseras and Fernández, 1995; Viseras et al., 1998). The Fonelas P-1 site is located palaeogeographically on the floodplain of this Axial System, near the mouth of a channel in one of the shallow lakes (Fig. 4).

The Axial or Longitudinal System was fed transversally by two other drainage systems made up of coalescing alluvial fans and named the Internal and External Transverse Systems (Viseras and Fernández, 1994, 1995), as their source areas lay within both the Internal Zones (Sierra Nevada and Sierra de Baza) to the South, and the External Zones (Sierra Arana, Montes Orientales, Sierra del Pozo and Sierra de Cazorla) to the North (Figs. 2 and 4). In the case of Unit VI (Late Pliocene─Pleistocene), the Axial System was located closer to the relief of the External Zones. This meant that the fans of the External Transverse System had a short radius (less than 3─4 km) and a wide sweep angle, whereas the fans of the Internal Transverse System had a 10─12 km radius and less sweep angle, coalescing to form a bajada system (Viseras and Fernández, 1992; Calvache and Viseras, 1997).

Progradation of the transverse systems led to local obstruction of axial drainage in the basin, which explains why some sectors of the main valley were temporarily occupied by small shallow lakes. Their shallowness and small size in relation to their alluvial feeder systems affected their ephemeral nature, subjecting them to frequent changes in depth and displacement of coastline (Fernández et al., 1993).

The literature contains numerous examples of vertebrate sites in sediments of the axial system of continental basins with this paleogeographic pattern, such as the Pliocene in the Aswash River basin in Ethiopia (Quade et al., 2004), the Miocene of the Siwalik Group in Pakistan or the Paleogene of the Bighorn Basin in Wyoming (Willis and Behrensmeyer, 1995).

The stratigraphic series of Unit VI at the Fonelas P-1 site is 70 m thick (fig. 5). There is alternation of detrital and carbonate sediments in fining-upward cycles 2 to 6m thick. As described in detail in previous studies of this basin (Fernández et al., 1996b; Viseras et al., 1998), this vertical succession of lithofacies with upward decreasing energy characterizes sedimentation of a meandering dominated floodplain (Allen, 1970; Alexander et al., 1994; Dalhoff and Stemmerik, 2000; Heydari and Townsend, 2001; Quade et al., 2004).

## 6. Facies associations related to the site

The Fonelas P-1 site lies on the intermediate part of one of the fining-upward cycles characterizing sedimentation in this sector of the basin. Palaeontological excavation of the site has identified several sections of different orientation distributed over approximately 30 $m^2$ (Fig. 6). It has therefore been possible to draw up several detailed stratigraphic logs lying very close together, establish a direct correlation between them and identify the lithofacies and 3-D geometry of the sedimentary bodies where the accumulation of large-mammal fossils is found (Figs. 6─8).

The five facies associations at the site (A─E) are described below and their significance is discussed in terms of sedimentary processes and fluvial environments.

### *6.1. Facies association A (channel filling)*

This association is located at the base of the cycle and where the bottom is visible it is a distinct erosive surface on the fine facies of the underlying sequence. This association contains the coarsest sediment: sand and granule lithofacies predominate, mostly showing sigmoidal cross-stratification (Sla lithofacies, Table 3) and therefore varying in thickness from 15 to 20 cm. Internal lamination is parallel to the base of the sigmoidal units and usually shows normal grading (Fig. 7b). The cross-stratification is partially destroyed by coarser grain (granule-pebble), lens-shaped bodies intercalated between the sigmoidal units, varying in thickness from 15 to 50 cm and extending laterally for 1 to 3 m, consisting of massive gravels with either trough or planar cross-stratification (simple lithofacies Gcm, and Gt or Gp, respectively) (Figs. 8a , 9c and 9d). Palaeocurrent data suggest a northeastwardly main flow direction (Fig. 9, log $S_2$b).

Following interpretations of other examples (Allen, 1970; Bluck, 1971; Nijnman and Puigdefábregas, 1978; Skelly et al., 2003), this association represents the filling of a sinuous channel in which lateral accretion predominated (Sla lithofacies), but where dunes that shifted downstream (lithofacies Gt), transverse bedforms (Gp) and a small amount of lag deposits (lithofacies Gcm) also occurred.

### *6.2. Facies association B (levee)*

This association occurs beside association A (channel filling), separated from it by an erosional scar inclined to the northwest (Fig. 9). It contains wedge-shaped bodies (Fig. 9b), up to 15 cm thick near the channel and decreasing progressively away from it. This eastward thinning of the wedges is supported by palaeocurrent data measured from current ripple cross-lamination (Fig. 9, log $S_2$a). The wedges are usually no more than 2 m wide and they thicken upwards. The lithofacies making up these bodies form two intervals of fining upward cycles: a lower one of horizontally laminated sand (Sh) or current ripples (Sr) and an upper one of horizontal or wavy laminated mud (Fl). The lower interval consists of pebble size clasts in only one of these cycles, with small-scale trough cross-lamination (Gt) representing the filling of a small, shallow erosional scar.

There is a 50-90 cm wide band between these wedges and the channel sediment (facies association A) where the beds of association B are intensely deformed and affected by multiple small slides, whose detachment surfaces are inclined in the same direction as the scar on the channel margin (Fig. 9a).

The similarity with other deposits (Alexander et al., 1994; Aslan and Blum, 1999) leads us to interpret facies association B as levee deposits on the floodplain closest to the channel. The erosion linked to the lateral displacement of this channel would have caused a steeply sloping, highly unstable margin where slides caused deformation of the levee deposits closest to the erosion margin, as described in classic examples (Bluck, 1971).

### *6.3. Facies association C (abandoned channel)*

This overlies association A with a gradational boundary between the two (Fig. 7a and log $S_1$). It consists of alternating layers of sand and mud in units from 5 to 25 cm thick and several metres wide, but no bigger than the channel in which association A developed. In the sandy layers, the grain size is medium and current ripples can be recognized (lithofacies Sr) indicating flow towards the NNE (Fig. 7, log $S_1$) and there is also horizontal lamination (Sh). The mud intervals show parallel or slightly wavy lamination (lithofacies Fl) with a base following the top of the sigmoids in the underlying association A (Fig. 9c) and with the top inclined less than the bottom, resulting in a spoon shape in vertical section. The southeastern part is thicker and the base and top are both concave upwards. Site excavation has exposed several square metres of the top of one of these mud layers, showing both current marks indicating

northeastwardly flow and traces formed by the passage of hyenas on a substratum consisting of mud beneath a shallow layer of water (Fig. 8c). The top of this layer, of which 18 $m^2$ have been mapped, also shows desiccation cracks in several places.

According to its types of lithofacies and the shapes of the sedimentary bodies they form, facies association C can be interpreted, as in other examples (Kraus and Wells, 1999), as the fill of a channel in a stage of gradual abandonment. During this process, periods of low energy traction flow (development of sandy layers with current ripples) alternated with periods of standing water, when fine sediments settled and clay plugs developed and which gradually filled the topographical depression of the old channel, as described by Guccione et al. (2001).

### *6.4 Facies association D (floodplain)*

This is located in gradual transition above facies association C. It is a series of cycles with two intervals: a lower one of horizontally laminated mud (lithofacies Fl) and calcium carbonate nodules, in places beginning with medium to fine sand with ripples (lithofacies Sr); and an upper interval of nodular limestone or marly limestone with abundant root traces (lithofacies Mr). These elementary mud-carbonate cycles recur four times (Figs. 7 and 8) with remarkable (tens of metres) extension. Disperse large mammal fossils are found, although no traces ahve been detected, unlike the case of the mud layers in facies association C.

Because of the similarity between these sediments and other examples described in the literature (e.g., Guccione et al., 2001; Retallack, 2001; Bridge, 2003), we interpret this facies association as floodplain deposits. By comparison with other outcrops in the basin, where this facies association can be traced by direct correlation to the channel whose overflow produced it (Viseras and Fernández, 1995; Viseras et al., 1998), we can estimate a distance of around one hundred metres from the sinuous active channel.

### *6.5. Facies association E (bioturbation)*

This occupies the same stratigraphic position as facies association C (abandoned channel) and is separated from it by a highly irregular surface (Fig. 7a). Facies association E is a ribbon-shaped body 25 to 40 cm thick and tens of centimetres wide mainly oriented SW-NE. The base has a very irregular morphology, while the top is

planar and horizontal. Seen in cross-section, the boundary surface of this body has vertical walls with scalloped morphology (small saw-toothed cavities) tens of centimetres thick (Fig. 7). The most characteristic lithofacies of this body are sub-angular, very irregularly sized clasts of mud from association C held in a matrix of sand, clay and silt (Fig. 8b). It has no internal organization (a massive or chaotic structure) and there are some rather thin layers of sand not more than 3 cm thick with ripples similar to the sandy intervals in facies association C (Sr). It should be pointed out that there is often lateral coincidence between the mud layers of association C and mud clasts with internal lamination in facies association E. The importance of association E is that it contains the large mammal fossil concentration with most elements and highest diversity of species at the Fonelas P-1 site (Fig. 8d).

We interpret this facies to be the result of animal bioturbation of the sediments of association C (abandoned channel) exposed to weathering and whose original features were completely destroyed by the effects of mammal passage, since we take the site, linked with facies association E, to be a hyena den where these animals were active (see more extensive comments in the discussion section). The excavating action of these animals' feet on a soft substratum (clay plugs) was the main cause of the massive or chaotic structure of association E. This interpretation is supported by two main pieces of evidence: 1) the presence of large mammal traces in the lutite interval of facies association C, immediately prior to association E and on which the latter lies in several places of the site and 2) the concentration of the most abundant accumulation of bones in the bioturbated lithofacies, as there is a direct relation between this lithofacies and the fossil record. Similar examples of deformation of soft sediments by passage of large vertebrates have been described in both modern and ancient fluvial and marginal lacustrine floodplain environments (Laporte and Behrensmeyer, 1980; Paik et al., 2001).

## 7. Discussion: evolution of sedimentary sub-environments and genesis of the site

The largest concentrations of bone remains at the Fonelas P-1 site appear in what we have described as facies association E, located in a very specific position in one of the characteristic cycles of the succession in Unit VI of this sector of the basin.

The simple lithofacies making up associations A to D, as well as the spatial relation between facies associations, allow us to reconstruct a logical series of sedimentary

events in this part of the Axial System lower basin (Fig. 10) as described below. The sedimentological evidence indicates that the area was crossed by a sinuous fluvial channel flowing north-eastwards which at this point made a convex curve towards the east (Fig. 10b). The reconstruction of this channel in the area excavated indicates a sinuous form, which is corroborated by the continuation of the sedimentary body to the north, where, several hundred metres from the site, another curve of the same channel can be reconstructed, in this case convex towards the west.

Unfortunately, neither the base of the channel nor the accretion margin developed during maximum fluvial activity are well exposed. However, the grain size of the sediment and the size of the bars and other bedforms suggest that this was not the main channel of the Axial System, but rather one of the many meandering secondary channels crossing the distal plain of the system (Fernández et al., 1996b; Viseras and Fernández, 1995) (Fig. 10a). Taking the data available from the outcropping part of this channel and by comparison with other well exposed examples in this sector of the basin (Viseras and Fernández, 1994; Viseras et al., 1998), we can estimate a size for this channel in bankfull state of 6-8 m wide and around 1.5 m deep (Fig. 10).

During maximum fluvial activity, processes of lateral accretion linked to a helical flow predominated in this channel, but the coarsest sediment was also carried downstream, mainly as sandy dunes. These processes resulted in the formation of facies association A (Fig.10b$_1$).

At high flow stage the channel overflowed spreading sandy and mudy sediment onto the floodplain and creating levees (facies association B) (Fig. 10b$_1$). Lateral accretion triggered the channel migration producing erosion of its eastern bank, which became unstable and suffered numerous small slides of the levee sediments into the channel bottom.

Local migration of the channel towards the east can be inferred for several reasons. The sigmoidal units are inclined in this direction and the progressive upward increase in thickness of the bodies interpreted as levees indicates the proximity of the channel to this sector of the floodplain. In addition, the destabilisation and steep slope of this margin are characteristic of an erosion margin in a meandering channel (Bluck, 1971).

The channel gradually filled with sediment, so that the base of the sigmoidal units of lateral accretion reached the erosion margin. From this point on, we can detect a decrease in the energy of the sedimentary processes in the channel, most probably due to the gradual deviation of flow to another position by chute cut-off. The former active

channel thus became a small depression filled by the clayey sediment settled from flood water, as described in examples such as the Mississippi River alluvial valley (Guccione et al., 2001), the Texas Coastal Plain (Aslan and Blum, 1999), the Rhine-Meuse Delta (Stouthamer, 2001) or ancient sediments (Dalhoff and Stemmerik, 2000; Nijnman and Puigdefábregas, 1978). In this phase, coinciding with the development of facies association C, we can estimate the residual channel to have been some 3 m wide and no more than 50 cm deep. Periods of flooding and settling would have alternated in this channel with periods of desiccation and low energy flow towards the NE. This was, therefore, a period when the channel acted as an ox-bow lake (Fig. 10$b_2$).

Finally, the clay plugs made the depression more shallow, the frequency of traction flows decreased, detrital sediment became scarce and chemical precipitation of calcium carbonate became important associated with the roots of the abundant vegetation growing in a floodplain subjected to prolonged periods of ponding (period of development of facies association D). Frequent ponding of the floodplain is consistent with the distal position in the fluvial system, where the gradient was very low and where proximity to the palustrine border of a lake resulted in a very high water table, so that no more than a slight increase in climatic humidity would make it rise, flooding the alluvial plain and expanding the palustrine border upstream. The literature contains many examples of similar interpretations of this lithofacies sequence (McGowen and Garner, 1970; Bluck, 1971; Jackson, 1976; Nijnman and Puigdefábregas, 1978; Miall, 1996; Stouthamer, 2001; Bridge, 2003, among others).

The remarkable facies association E (bioturbated) is clearly not linked to this evolution of purely fluvial processes. Moreover, it does not appear in the other cycles of the succession. The fact that it is coetaneous with association C (abandoned channel) means we can genetically link the animal bioturbation with the last stages of the channel's evolution. Thus, the slight depression formed by the residual channel in the stage of abandonment (ox-bow lake), occasionally ponded by both rainwater and overflow from the nearby active channel, would have been a relatively protected area, with easy access to water for the animals, probably used by some (carnivorous scavengers) as feeding place and den. This hypothesis of a hyena den is also based on data such as those of Table 2, which show intensive feeding on bones by scavenging carnivores, as well as the fact that the animals did not die at the site (with the possible exception of *Pachycrocuta brevirostris* cubs). Passage of animals over such a depression with a very soft substratum would have caused a very dense pattern of

tracks, creating narrow corridors with an intensely bioturbated bottom, coinciding approximately in orientation with the abandoned channel (Fig. 10b$_2$). After complete filling of this residual channel, the topography would have been homogenized at the level of the floodplain (Fig. 10b$_3$). This is why the particular location of the site ceased to be a preferential occupation zone for the animals, just at the beginning of the development of facies association D (floodplain). At this point, the main animal occupation must have transferred to another place providing the topographical conditions described above. The high sedimentation rate in the abandoned channel, resulting from both the local concentration of sediment from rainfall and detrital supply from overflow of the active channel in its new position (about a hundred metres from its previous position), and from chemical precipitation of the floodplain, led to the burial of the fossil accumulations. This genetic context characterizing the site remained outside the erosive influence of fluvial channels, which were displaced tens or hundreds of metres from the abandoned channel. Consequently, the position of this site in the context of the local evolution of an alluvial channel abandoned by avulsion coincides with that of other vertebrate sites described in the literature (Behrensmeyer, 1988; Behrensmeyer et al., 1995; Quade et al., 2004).

## 8. Conclusions

The main results of the study are the following:

1. On the scale of the general palaeogeography of the basin, the Fonelas P-1 site is located on the distal stretch of the axial drainage system of the Guadix Basin, near its connection to a shallow lake, occupying a palaeogeographic situation similar to that of many other vertebrate sites.

2. The site is located in a sedimentary cycle typical of a meandering fluvial system. This cycle consists of four facies associations related to fluvial processes: (A) gravel and/or sand in layers with sigmoidal geometry, caused by the lateral accretion in a sinuous channel, (B) sand and mud in wedge-shaped bodies abutting onto the erosion bank of the channel, interpreted as levee deposits, (C) fine sand and mud with sigmoidal laminae, gradually overlying the facies A and representing progressive channel abandonment deposits, (D) mud and carbonate in extensive horizontal layers lying directly on the C facies and recording typical floodplain sedimentation.

3. The main accumulation of large mammal fossils is found in a facies genetically independent of those described above, as it is unconnected with purely fluvial processes. This new facies (E) consists of very angular clasts of mud of facies C (channel abandonment) with no internal organization, held in a matrix of sand, silt and clay and is interpreted as the result of bioturbation of a soft substratum by continuous passage of large mammals (carnivorous scavengers, specifically hyaenids) in an occupation space.

4. The detailed palaeogeographic context inferred for facies E is that of an abandoned meander. This would have formed a slight topographic depression that was periodically flooded, either by rainfall or by small overflow from the distant active channel, and occupied by hyenas.

5. The type of facies represented by association E has never before been identified and described in continental basin filling. Its sedimentological and palaeobiological importance is due to the fact that these are biogenetic facies characteristic of the biological activity of large scavenging carnivores on fluvial substrata. Whether they present fossil content or not, they are predictive, as they indicate sedimentary interruption, subaerial exposure and biological occupation wherever they may be identified in the geological record. Recognition of this facies association can be used as a sedimentological criterion for prospecting large mammal activity in future palaeontological research. .

## Acknowledgments

This study has been financed by research projects BTE2001-2872, CGL2005-06224/BTE (MEC, FEDER), IGME 2001-016, IGME 2005-009, Working Groups RNM-163JA and RNM-200JA and the Consejería de Cultura of the Junta de Andalucía. We are grateful to all our colleagues on the Fonelas project for their efforts and their enthusiasm during the arduous excavation seasons and to Prof. Juan Fernández for his advice on sedimentological matters. The study has been considerably improved thanks to the suggestions of F. Surlyk and two anonymous reviewers. We are also grateful to Dr. Ian MacCandless for his translation of this paper. Finally, we are indebted to Dr.

Gary J. Nichols (Royal Holloway University of London) for reviewing in a careful and unselfish way both the language and the geological aspects.

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**Figure captions**

Fig. 1. Excavation grid at the Fonelas P-1 site. The fossil-bearing layer (facies E) is not continuous either horizontally or vertically, but wherever it appears it contains a large-mammal fossil record. The clay plug or sandy units between which this facies intercalates are void of vertebrate bone remains. The column indicates other layers

(LC, ES and AN) with a sporadic palaeontological record that are genetically independent of that located in facies E. The stratigraphic log on the right is reproduced in more detail with an explanation in Fig. 7.

Fig. 2. Geological maps of the Betic Cordillera and Guadix Basin. The location of Fonelas village, close to the Fonelas P-1 large-mammal site, is indicated in the lower map.

Fig. 3. Stratigraphic units filling the Guadix Basin (after Soria et al., 1999, modified). Notice the location of the Fonelas P-1 site in unit VI.

Fig. 4. Palaeogeography of the Guadix Basin during deposition of Unit VI (Late Pliocene–Late Pleistocene). Notice the location of Fonelas on the Axial System, close both to the External Transverse System and to one of the small ephemeral lakes occupying the axial valley.

Fig. 5. General stratigraphic log of Unit VI next to the Fonelas P-1 site.

Fig. 6. Location of the stratigraphic logs (Figs 7., 8 y 9) in the excavation.

Fig. 7. Detailed stratigraphic log S1 (see location in sketch, upper left) and photographs of the facies associations described in the text.

Fig. 8. Detailed stratigraphic logs $S_3$a and $S_3$b (see location in the sketch, upper left) and photographs of the facies associations described in the text.

Fig. 9. Detailed stratigraphic logs $S_2$a and $S_2$b (see location in the sketch, upper left) and photographs of the facies associations described in the text.

Fig. 10. Reconstruction of the sedimentary environment of the Fonelas P-1 site. A: axial valley with meandering channels (Axial System) between the alluvial fans of the Internal and External Transverse Systems (see palaeogeographic sketch of Fig. 4). B: laterally migrating sinuous channel abandoned in one meander by chute cut-off. This is the place occupied by large mammals. B1, B2 and B3: location of the

facies associations throughout three evolutionary stages of the channel, active (B1), abandoned (B2) and establishment of floodplain conditions (B3).

Table 1. Faunal assemblage identified at Fonelas P-1 site.

Table 2. Summary of the provisional taphonomic data of the Fonelas P-1 site (samples from 2001 and 2002 seasons). Overall analysis of the variables suggests that the site represents a secondary association, collected by scavengers, with very rapid burial of the bone remains. (NISP: number of identifiable specimens; MNI: minimal number of individuals) (1: Secondary association, collected by scavengers, 2: No hydraulic sorting, 3: Very short period of subaerial exposure before burial).

Table 3. Characteristics and interpretation of the lithofacies accompanying the Fonelas P-1 site.

Figure 1

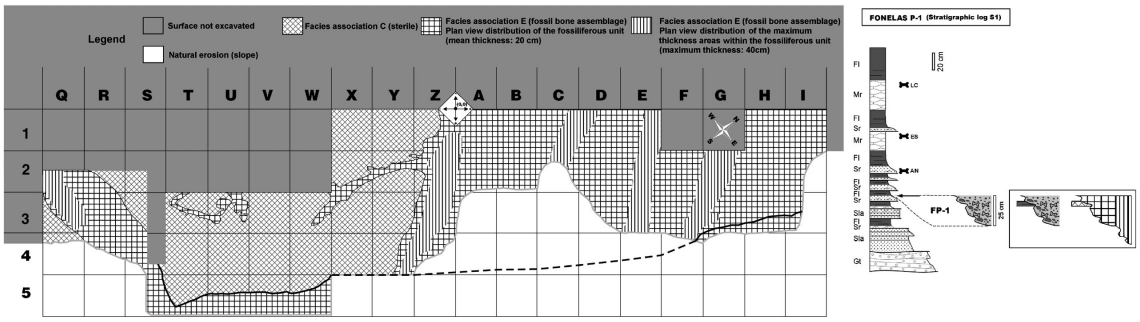

Figure 2

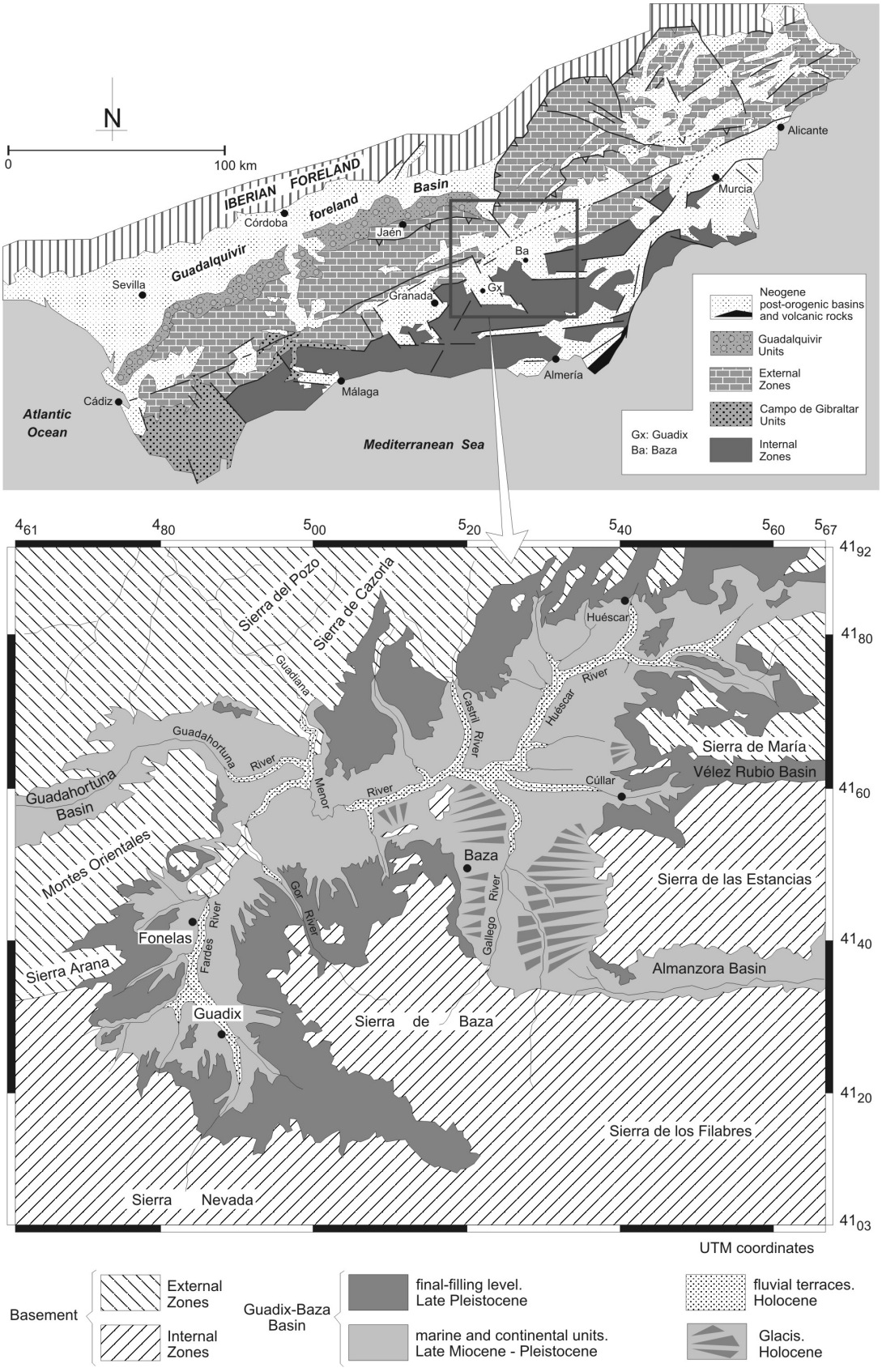

Figure 3

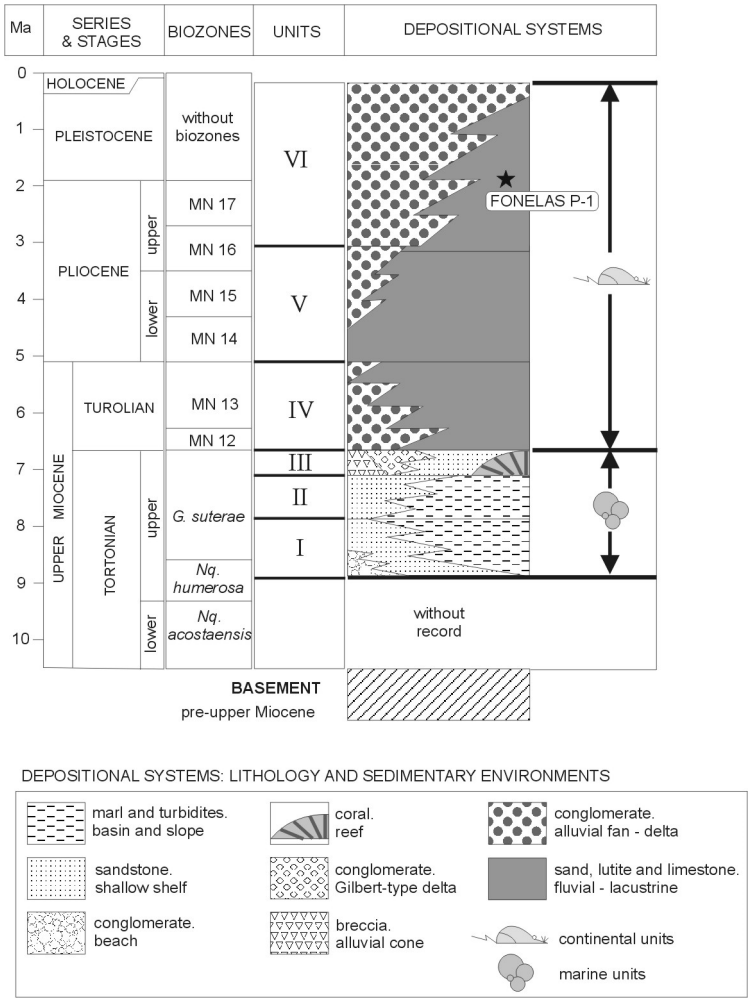


Figure 4

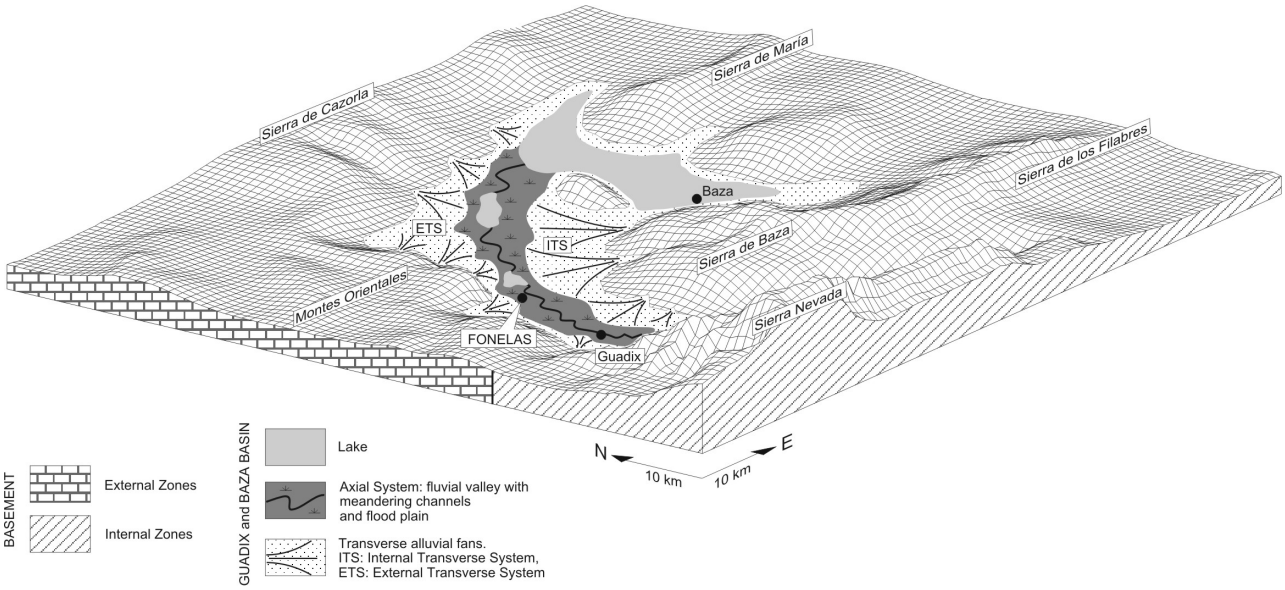

Figure 5

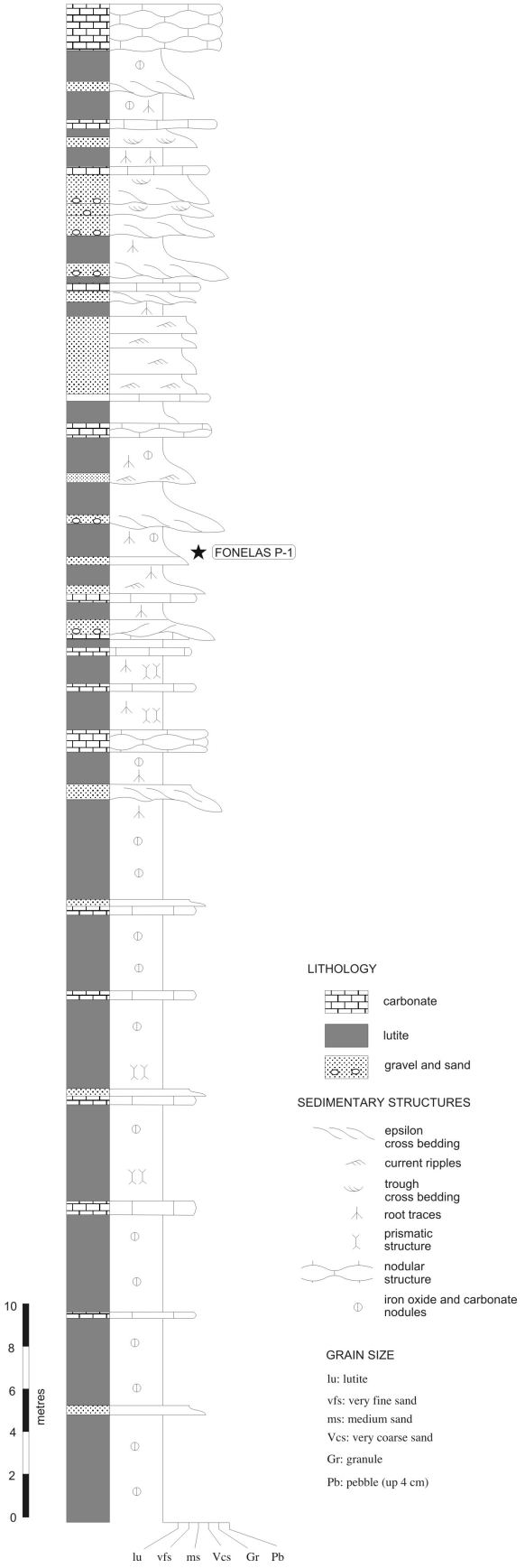

Figure 6

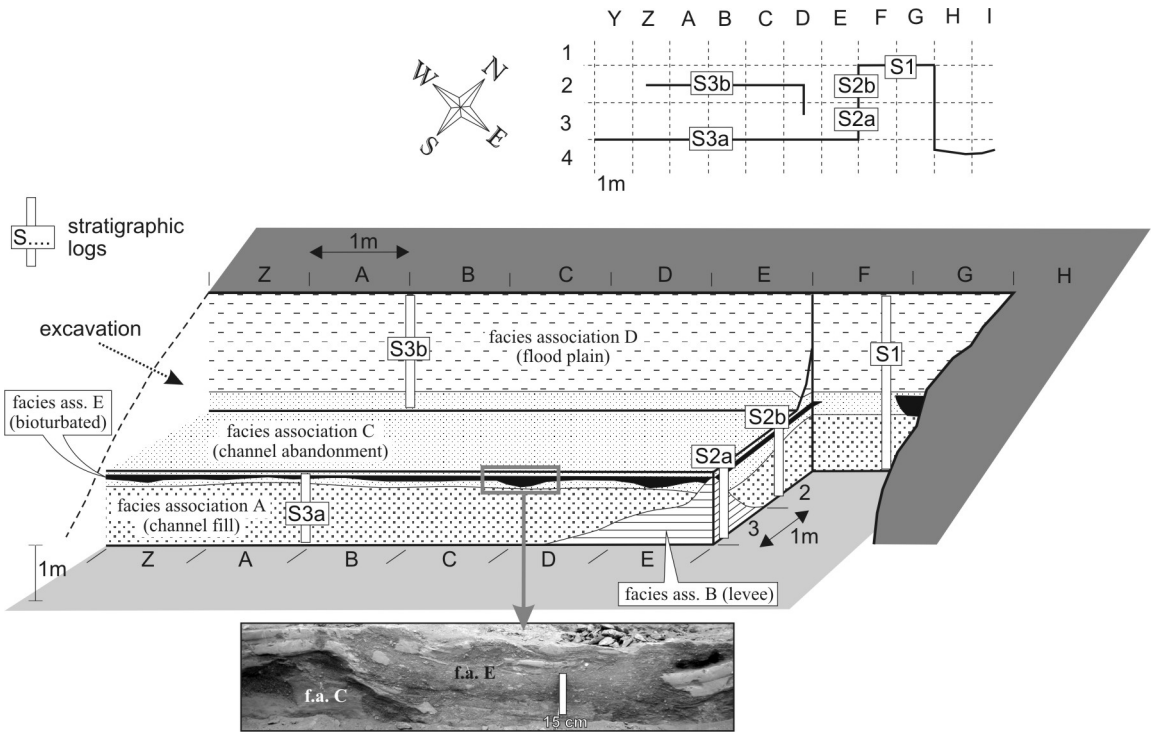


Figure 7

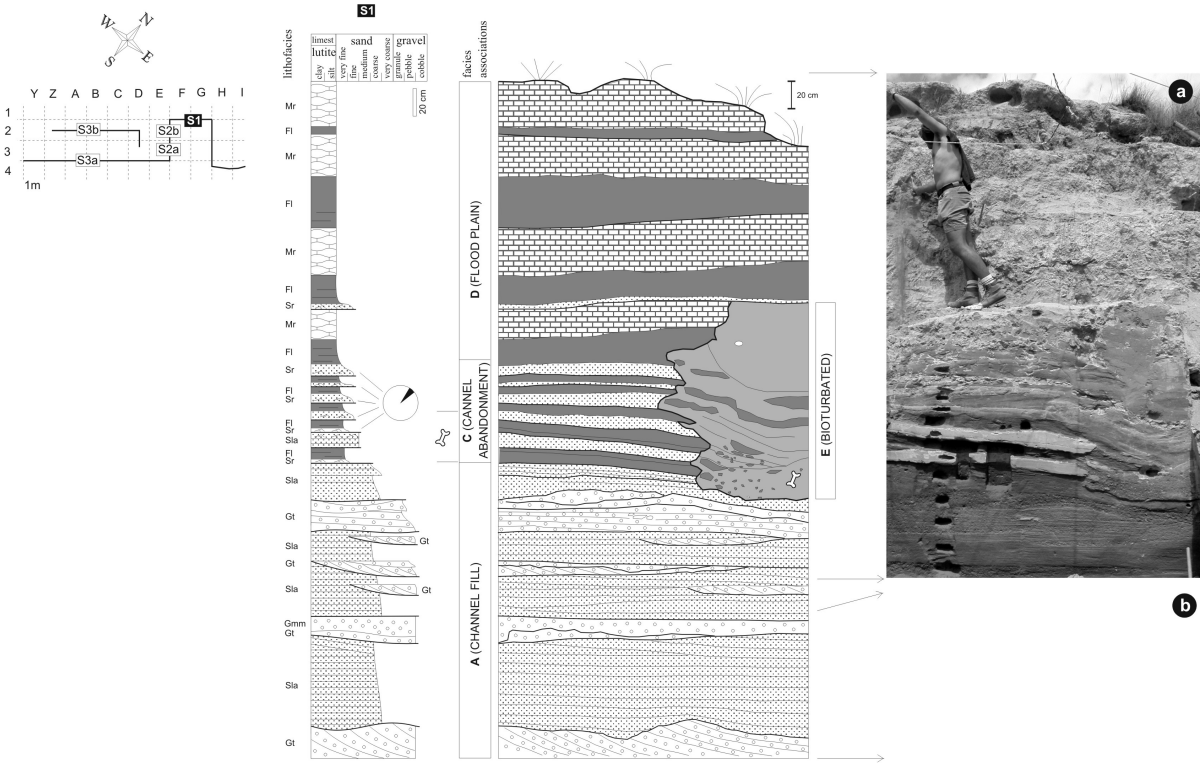

Figure 8

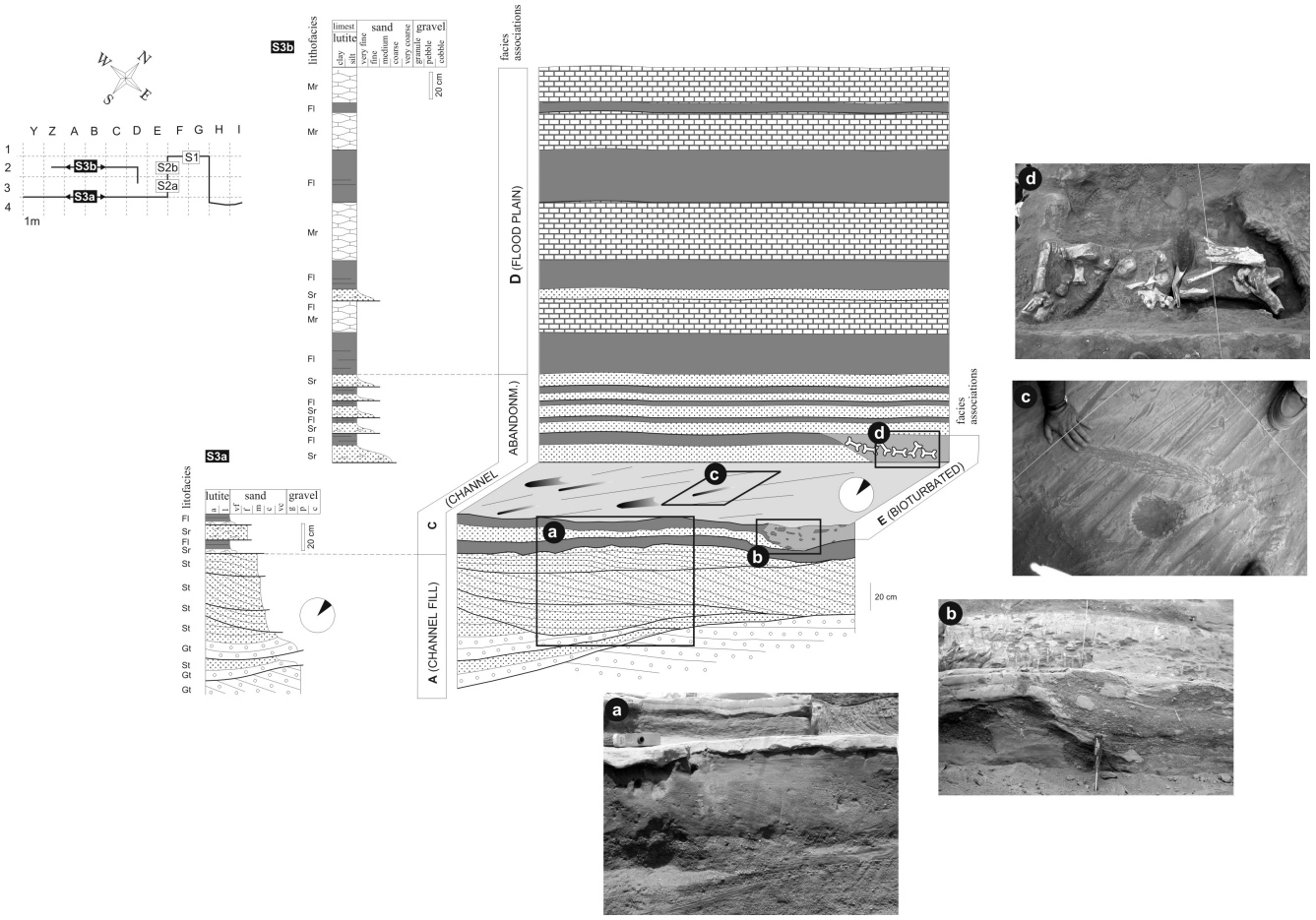


Figure 9

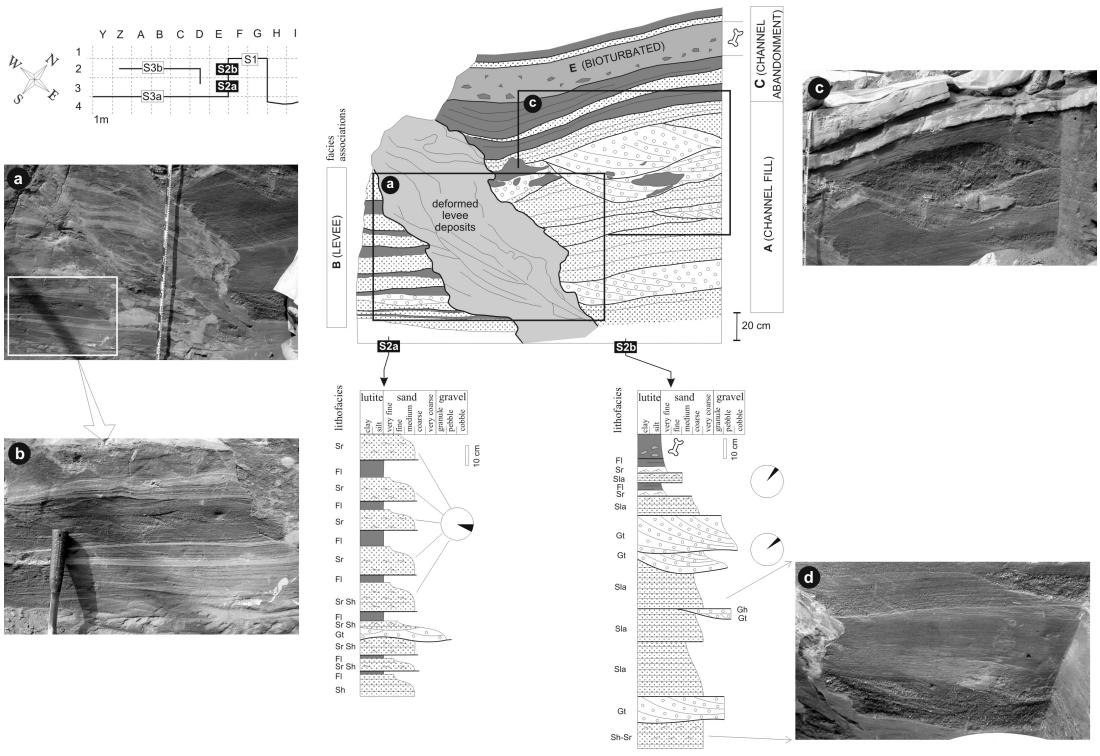

Figure 10

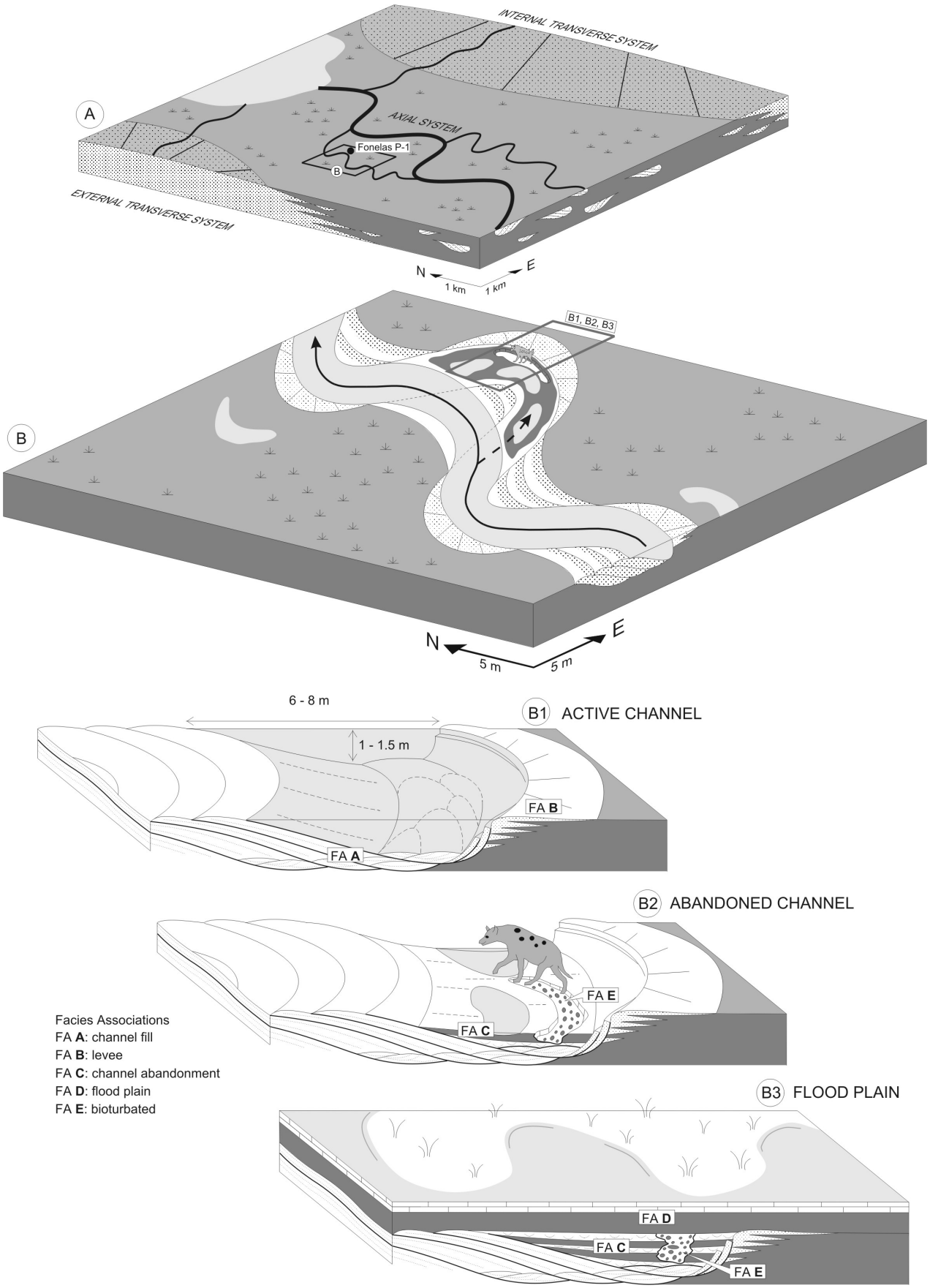

Table 1

| LARGE MAMMALS | SMALL MAMMALS | REPTILS | BIRDS |
|---|---|---|---|
| *Meles* nov. sp. | *Mimomys* sp. | *Testudo* sp. | Bird gen. indet. |
| *Vulpes alopecoides* | *Castillomys* cf. *rivas* | Colubridae gen. indet. | |
| *Canis* nov. sp. | *Apodemus* sp. | | |
| *Canis etruscus* | *Stephanomys* sp. | | |
| *Canis (Xenocyon)* cf. *falconeri* | *Eliomys* sp. | | |
| *Lynx pardinus* | *Prolagus* cf. *calpensis* | | |
| *Acinonyx pardinensis* | *Oryctolagus* cf. *lacosti* | | |
| *Megantereon cultridens* | *Erinaceus* cf. *europaeus* | | |
| *Homotherium latidens* | | | |
| *Hyaena brunnea* | | | |
| *Pachycrocuta brevirostris* | | | |
| *Croizetoceros ramosus* | | | |
| *Cervus? rhenanus philisi* | | | |
| *Eucladoceros* sp. | | | |
| *Capra* nov. sp. | | | |
| *Gazella?* nov. sp. | | | |
| *Gazellospira* nov. sp. | | | |
| *Leptobos etruscus* | | | |
| *Praeovibos* nov. sp. | | | |
| *Mitilanotherium* nov. sp. | | | |
| *Potamochoerus* nov. sp. | | | |
| *Equus major* | | | |
| *Stephanorhinus etruscus* | | | |
| *Mammuthus meridionalis* | | | |

Table 2

| | | | | |
|---|---|---|---|---|
| **ASSEMBLAGE DATA** | **NISP (taxonomic identification) (1375)** | Carnivora NISP | | 9.0 % (1) |
| | | Artiodactyla NISP | | 40.0 % |
| | | Perissodactyla NISP | | 13.0 % |
| | | Proboscidea NISP | | 1.0 % |
| | | Other groups NISP | | 11.0 % |
| | | Uncertain specimens | | 26.0 % |
| | **Body weight range** | < 0.2 - > 3000 Kg (1,2) | | |
| | **Number of species (35)** | Micromammal species (rodents in disgregated coprolites) | | 8 |
| | | Macromammal species | | 24 (1,2) |
| | **Macromammal MNI (84)** | Carnivora MNI | | 23.0 % (1) |
| | | Artiodactyla MNI | | 58.0 % (*Gazellospira* 30 %) |
| | | Perissodactyla MNI | | 17.0% |
| | | Proboscidea MNI | | 2.0 % |
| | **Carnivore/ungulate index [f(MNI)]** | 29.2 % (1) | | |
| | **Macromammal age spectrum** | Infant | 26.0 % (1) [(Hyaenidae, *Pachycrocuta* 2.4%) *(Gazellospira* 9.5 %)] | |
| | | Juvenile | 5.0 % (1) | |
| | | Adult | 68.0 % (*Gazellospira* 20.2 %) | |
| | | Senile | 1.0 % | |
| | **Bone articulation** | 4.0 % (1) | | |
| | **Grouping** | 20.0 % | | |
| | **Sedimentary infilling** | 5.0 % (3) (only in broken bones; periosteum sheath present at burial) | | |
| | **Sedimentary infilling/ matrix congruence** | 100.0 % | | |
| | **Reworked bones** | 0.0 % | | |
| | **Skeletal parts** | Bone size range | 1.1-58.3cm (2) | |
| | | Deer antlers | 0.3 % | |
| **BONE MODIFICATION DATA** | **Bone completeness** | Bone (1) (including craneal elements) (73.0 %) | Complete (limb+girdle bones) | 40.0 % |
| | | | Fragment (limb+girdle bones)<br>· Proximal epiphyses<br>· Shaft<br>· Distal epiphyses | 60.0 %<br>39.0 %<br>22.0 %<br>39.0 % |
| | | Isolated teeth | | 10.0 % |
| | | Splinter (spiral and/or longitudinal fractures) | | 17.0 % (1) |
| | **Marks** | Abrasion/ polished | | 0.0 % (2) |
| | | Weathering stage<br>· 0-1<br>· 2-3<br>· 4-5 | | <br>94.1 % (3)<br>5.2 %<br>0.6 % |
| | | Fossil root marks | | 0.0 % (3) |
| | | Modern root marks (fossils associated with the natural slope) | | 20.0 % |
| | | Digestive corrosion | | 5.0 % (1) |
| | | Fossil insects | | 0.6 % |
| | | Modern insects | | 0.1 % |
| | **Biostratinomic breakage** | Longitudinal | | 14.0 % (1) |
| | | Type II Spiral | | 26.0 % (1) |
| | **Fossildiagenetic breakage** | Ortogonal (manifold features) | | 57.0 % |
| | **Traces** | Gnawing marks (tooth marks)<br>· Micro rodents<br>· Macro rodents<br>· Canids<br>· Felids<br>· Hyaenids | | <br>0.0 %<br>0.0 %<br>0.0 %<br>0.1 %<br>37.0 % (1) |
| | | Cut marks (hominids) | | 0.0 % |
| | | Trampling marks [f(matrix composition)] | | 0.4 % |
| | **Size of accumulation** | ca. 800 $m^2$ | | |

| | | | | |
|---|---|---|---|---|
| **QUARRY DATA** | **Excavated surface** | ca. 43 $m^2$ | | |
| | **Fertile surface (facies association E) (ca. 25 $m^2$)** | Mean thickness | 20 cm | |
| | | Density | ca. 70/$m^2$ | |
| | | Orientation | 40% with preferred orientation | |
| | | Dip | Assemblage average | Sub-horizontal; 8º (2) |
| | | | Isolated bones average | Horizontal; 3º (2) |
| | | | Grouping bones average | Sub-horizontal; 15º (2) |
| | | | Patchiness | Highly patchy |
| | **Lithology and other stratigraphical aspects in the text** | | | |

Table 3

| Facies code | Grain size | Sedimentary structures | Characteristics of the beds | | | Interpretation | Subenvironment |
|---|---|---|---|---|---|---|---|
| | | | Shape | Thickness (cm) | Lateral extent (m) | | |
| Gcm | pebble to cobble | massive, weak imbrication | lens | 15-20 | 0,5-1 | lag deposits | active channel |
| Gt | granule to pebble | through cross beds | lens | 15-50 | 1-3 | minor channel fill, sinuous crested (3D) dune | active channel, levee |
| Gp | pebble | planar cross beds | lens | 15-50 | 1.5-3 | transverse bedforms, straight crested (2D) dune | active channel |
| Sla | coarse sand to granule | epsilon cross-bedding | sigmoidal | 15-20 | 2-4 | lateral accretion deposits | active channel |
| Sh | very fine sand to coarse (may be granule) | horizontal lamination | wedge/ sheet | 5-10 | < 2 | upper flow regime | levee (lower part), abandoned channel |
| Sr | fine to medium sand | ripple cross-lamination | wedge | 10-15 | 1-2 | lower flow regime | levee, abandoned channel, flood plain |
| Fl | silt-mud | even/ wavy lamination, very small ripples, dessication cracks | wedge/ spoon | 5-25 | 2-6 | lower flow regime, wanning flood deposits, clay plug | levee (upper part), abandoned channel, flood plain |
| Mr | marl-limestone | roots, nodules, Fe oxide | sheet (irregular) | 20-50 | > 100 | incipient soil with chemical precipitation | distal flood plain, palustrine fringe |